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ROOT RESERVES OF SOUTH AFRICAN HIGHVELD
GRASSES IN RELATION TO FERTILIZING AND
FREQUENCY OF CLIPPING.

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INTRODUCTION.

The influence of cutting treatments on herbage growth and root development of grasses has been studied by many workers in various countries. Earlier literature on this subject has been reviewed by Graber (3), Robertson (15), and Biswell and Weaver (2). The latter report that "investigators are in agreement that the more frequent and drastic the cutting treatment the less is the yield of tops, rhizomes and roots."

Experimenting with six North American prairie grasses Biswell and Weaver (2) found that the root weight of plants clipped four to seven times at fortnightly intervals averaged only ten per cent. of that of unclipped control plants; the species investigated were *Andropogon furcatus*, *Bulbilis dactyloides*, *Panicum virgatum*, *Poa pratensis*, *Andropogon scoparius*, *Bouteloua gracilis* and *Bouteloua curtipendula*. Robertson (15) studied the response of six range and pasture grasses, viz. *Poa pratensis*, *Bouteloua gracilis*, *Koeleria cristata*, *Stipa spartea*, *Bromus inermis* and *Holcus sorghum sudanensis*. Four clippings reduced root growth in these species about twice as much as that of tops; the roots of the clipped plants ranged in weight from one-third to one-fiftieth as much as those of their controls. Similar results were obtained by Graber (3) with *Poa pratensis*, *Agrostis alba* and *Phleum pratense*. In *Phalaris tuberosa* (13) cutting five times reduced the yield of herbage by 54 per cent., and the root system by 78 per cent. Sturkie (18) found that the root stock development of *Sorghum halepense* was reduced by any cutting treatment and that the degree of reduction increased with the frequency of cutting. According to Hase (7) clipping decreased length and spread of the roots of *Buchloe dactyloides*, *Bouteloua gracilis* and *Bouteloua curtipendula*.

A number of workers have also demonstrated that the reduction in

root and rhizome weight will be the greater the shorter the grass is cut. According to Stapledon and Milton (17) the root weight of *Dactylis glomerata* plants cut every three weeks to ground level was only about one third of that of plants clipped every three weeks to a height of six inches. In experiments carried out by Graber and Ream (4) *Poa pratensis* invariably formed less roots and rhizomes when cut to a height of $\frac{1}{2}$ inch than when cut to a height of $1\frac{1}{2}$ inches. In *Festuca rubra*, *Poa pratensis* and *Agrostis capillaris* Harrison (5) found that "the shorter the grass was cut and the more leaf area was reduced, the smaller was the quantity of roots produced." The same response was shown by various *Agrostis* species and *Festuca duriuscula* (16), *Phleum pratense* and *Lolium perenne* (14), *Lolium italicum* and *Festuca pratensis* (19).

The results of certain investigations indicate the existence of interactions between clipping and other factors affecting growth, particularly nitrogen supply. Graber and Ream (4) concluded from their work on *Poa pratensis* that only when a productive level of reserves was maintained by height or infrequency of cutting did the plants utilise an abundance of nitrogen to produce abundant vegetative growth. Harrison (5) found that application of mineral fertilizers did not compensate for a lack of top growth in the production of roots in the grasses investigated; on the contrary, addition of ammonium sulphate to closely clipped plants of *Festuca rubra* and *Poa pratensis* resulted in a further decrease in their root weight, whilst plants of *Agrostis capillaris* were even killed by this treatment. Growing *Poa pratensis* under controlled conditions in the greenhouse, Harrison (6) was later able to confirm that the addition of nitrogen tends to aggravate the deleterious effects of frequent clipping on the root system. Plants supplied with nitrogen died after fourteen clippings at weekly intervals, whilst plants without additional nitrogen supply survived the same cutting treatment. Abundant nitrogen supply, particularly when combined with optimal temperatures, led to rapid vegetative regeneration resulting in a reduction of the weight of roots and rhizomes, presumably due to excessive mobilisation and exhaustion of carbohydrate reserves. Similarly, Johnson and Dexter (8) found that frequent and short cutting was very injurious to plants of *Agropyron repens* receiving an abundant supply of nitrogen, but caused only slight injury to "minus-nitrogen" plants. The authors consider that the stimulation of vegetative growth by nitrogen under conditions of frequent and close cutting resulted in a depletion of organic reserves stored up in roots and rhizomes, eventually leading to carbohydrate starvation and death.

That excessive defoliation results in a depletion of organic food reserves in the underground parts is indicated by the results of chemical

analyses carried out by several workers. Aldous (1) showed that in composite root samples of prairie grasses the percentages of total sugars, starch and dextrin decreased with the frequency of cutting, "the greatest amounts being present in the roots of plants that had not been cut or that had been cut less frequently and at the greatest heights." According to McCarty (9) one clipping carried out at different times of the season lowered in almost every case the percentage of sugars and starch present in stem bases and roots of *Elymus ambiguus* at the end of the season. In a later investigation the same author (10) demonstrated that three clippings at five-day intervals during spring removed one third of the amounts of sugars and starch stored up in the stem bases and roots of *Bromus carinatus*. In a further contribution McCarty and Price (11) report that the amounts of reserve carbohydrates (mainly sucrose and starch) in stem bases and roots of *Bromus carinatus* and *Agropyron tenerum* were lowered by all the clipping treatments employed; the degree of reduction depended on the time, frequency and closeness of cutting. The level of root reserves was lowest in plants continuously clipped short. In *Agropyron spicatum* (12) clipping to crown level at two-weeks intervals during eight weeks of the vegetative stage reduced the proportion of storage carbohydrates by fifty per cent. as compared with unclipped control plants.

In a recent investigation the writer (22) subjected South African Highveld grassland vegetation to a series of clipping treatments for two years. It was found that root weights as well as percentages of sugars and starch in the roots decreased progressively with the frequency of clipping. Cutting at monthly intervals reduced the total dry matter of the roots on an average by 63.8 per cent. and the combined amounts of sugars and starch by 76.6 per cent. as compared with one clipping per year. Fertilizer treatment was not able to counteract the damage to root development and the exhaustion of root reserves brought about by frequent defoliation.

The present contribution reports the results of an experiment designed to test the effects of various frequencies of cutting, with and without fertilizer treatment, on root development and carbohydrate reserves of five important South African Highveld grasses.

EXPERIMENTAL METHODS.

The experiment was conducted at Frankenwald, the Botanical Research Station of the University of the Witwatersrand, near Johannesburg. On a piece of undisturbed veld, which had been subjected to un-

controlled light grazing for some years, six plots were laid out in winter 1939, after old growth had been removed by burning.

The soil of the area is an acid loamy sand of about twelve inches depth on decomposed granite. The soil is poor in organic matter, nitrogen and phosphorus; the pH is 5.4. The results of an analysis of the surface soil are given in Table I.

TABLE I.

RESULTS OF SOIL ANALYSIS. .

Percentages of Dry Fine Earth.

Sand	75.2	Loss on Ignition.. ..	3.9
Silt.. .. .	13.0	Nitrogen	0.086
Clay	11.8	Phosphoric Oxide	0.016
Total Colloids	13.4	Potash	0.063
Maximum Water Retain- ing Capacity	42.4		

Three of the above-mentioned six plots were not fertilized (O), whilst the other three plots received a well-balanced fertilizer treatment (NPK) during the two seasons 1939-40 and 1940-41. The amounts of fertilizer applied per morgen during each season were:—

800 lbs. of Kynoch Grass No. 1, equivalent to 120 lbs. P_2O_5 , 40 lbs. N and 40 lbs. K_2O . This fertilizer was spread each year in spring. In addition, two dressings of 200 lbs. of ammonium sulphate per morgen (= 42 lbs. N per dressing) were applied at convenient intervals during the season.

The rainfall amounted to 32.3 inches in 1939-40 and to 35.8 inches in 1940-41.

Five quadrats, each two square metres in extent, were pegged out in each of the six plots. During both seasons these quadrats were subjected to different clipping treatments, as follows:—

Number of Clippings per Season.

Quadrat No. 1 : One (in the beginning of April).

Quadrat No. 2 : Two (in the middle of December and April).

Quadrat No. 3 : Four (at two-monthly intervals, namely in November, January, March and May).

Quadrat No. 4 : Nine (at monthly intervals from September to May).

Quadrat No. 5 : Sixteen (at approximately fortnightly intervals during the months of September to May).

Clipping was carried out with sickles and scissors, the herbage being removed as completely as possible. The clipped herbage was collected, dried, weighed and chemically analysed. These herbage data have been published elsewhere (23), and will be discussed here only as far as they have a bearing on the results reported in this paper.

At the end of the period of treatment root samples were taken of the five dominant grass species in the area, namely *Trachypogon plumosus*, *Tristachya hispida*, *Eragrostis chalcantha*, *Brachiaria serrata* and *Digitaria tricholaenoides*. The first four of these grasses are typical tufted grasses, whilst *Digitaria tricholaenoides* forms irregular mats by means of rhizomes. In order to obtain comparable data of root weights it was decided to base root weights on basal area in the case of the four tufted grasses. For this purpose, the outlines of a number of tufts of each species were traced at the beginning of the experiment on celloidin paper mounted on a sheet of glass. Generally, a total of twelve or more tufts per species and treatment, distributed over the three quadrats of the same treatment, were traced in this way. At the same time the exact position of every traced tuft was entered on a map for each quadrat so that the plants could be found again for subsequent collecting of the roots. The traced tuft areas were also measured by planimeter. In the winter of 1941, after the clipping and fertilizer treatments had been continued for two seasons, the roots of the marked plants were dug out to a depth of four inches. The individual root samples of the same species and treatment were combined to form one sample and, since the total basal area was known, the root weight of one square decimetre basal area could be calculated.

This procedure was not possible with *Digitaria tricholaenoides*. Here, relatively big samples were taken of both roots and rhizomes from the upper four inches of the soil. After the material had been killed and dried (see below), the roots were separated from the rhizomes and both were weighed. By measuring the total length of the rhizomes of each sample or of a weighed aliquot thereof, the weight of one metre rhizome length and the root weight per metre rhizome length could be calculated. Thus, whilst the figures for the weights of the *Digitaria* roots cannot directly be compared with those of the other grasses, they are at least comparable with one another.

All root and rhizome samples were—as far as possible—freed from adhering soil, killed by autoclaving for five minutes at five lbs. pressure, dried at a temperature of about 60°C, weighed and ground for chemical analysis. Reducing and non-reducing sugars, starch (including dextrin) and acid-hydrolysable polysaccharides were determined, using essentially

the same methods as previously employed by the writer (22). In order to eliminate errors due to adhering soil all chemical constituents were expressed as percentages of combustible dry matter; root and rhizome weights were likewise calculated as combustible dry matter.

DISCUSSION OF RESULTS.

Root and Rhizome Weights.—The root and rhizome weights are shown in Table II and Fig. 1. All root weights decreased with increased

TABLE II.
ROOT AND RHIZOME WEIGHTS.

ROOT WEIGHTS IN GRAMS OF COMBUSTIBLE DRY MATTER PER ONE SQUARE DECIMETRE BASAL AREA.

Number of cuts per season.		1	2	4	9	16
Trachypogon pl. ..	O	4.78	5.37	2.80	0.85	0.66
	NPK	6.73	5.62	3.00	0.63	0.42
Tristachya hisp. ..	O	4.92	6.50	3.85	2.54	2.26
	NPK	7.62	9.60	7.33	1.85	1.21
Eragrostis chale. ..	O	3.64	3.66	2.42	0.28	0.02
	NPK	7.38	9.90	2.45	0.27	0.04
Brachiaria serr. ..	O	10.20	15.33	1.68	0.63	2.16
	NPK	12.32	11.23	1.53	1.09	1.01

ROOT AND RHIZOME WEIGHTS OF *Digitaria tricholaenoides* IN GRAMS OF COMBUSTIBLE DRY MATTER PER ONE METRE RHIZOME LENGTH.

Number of cuts per season.		1	2	4	9	16
Roots	O	0.61	0.59	0.48	0.27	0.18
	NPK	1.57	1.63	0.99	0.26	0.09
Rhizomes	O	10.78	10.71	10.77	7.90	8.14
	NPK	13.54	13.23	7.90	6.82	6.28

frequency of clipping. The root weights of plants clipped twice a year were in some cases higher than those of plants cut once a season, in other cases they were equal or not appreciably lower. Very significant reductions in the root weights were, however, brought about when the herbage was cut four times per season or more often. In the case of *Eragrostis chalcantha* plants cut sixteen times a year only traces of roots were found.

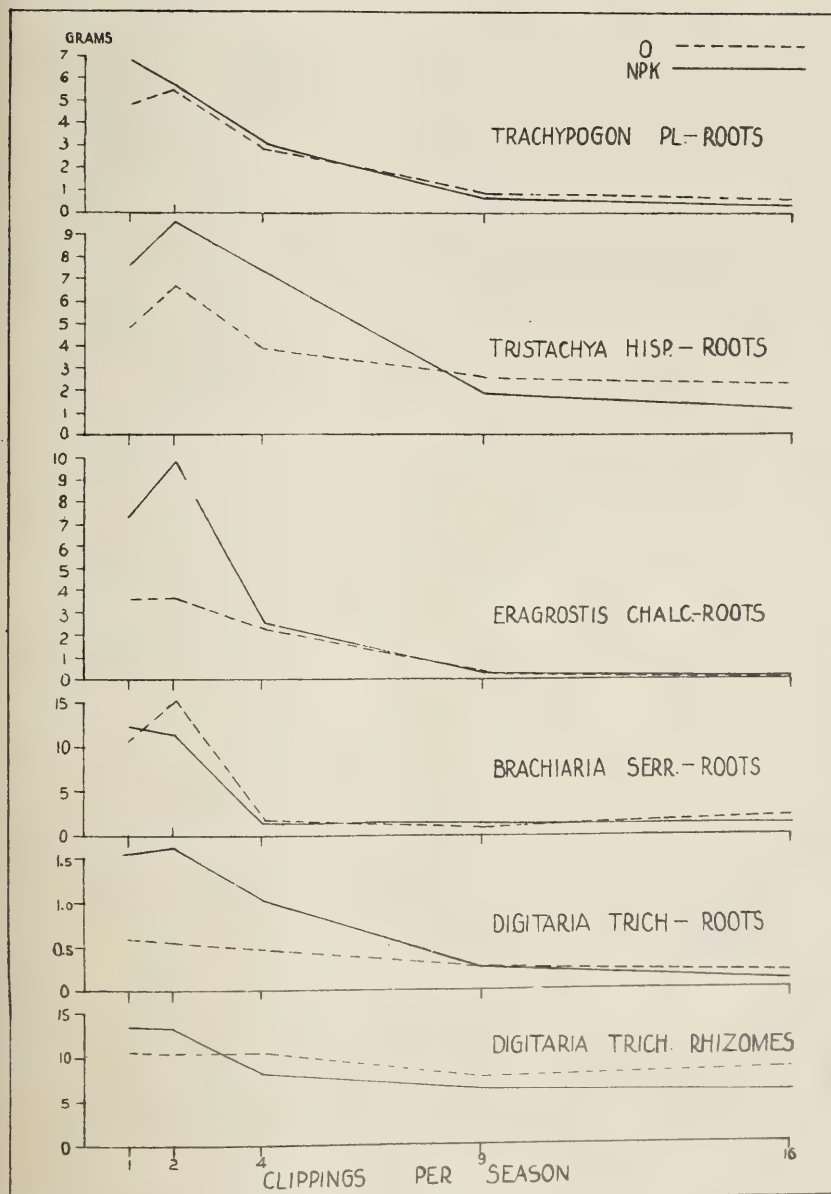


FIG. 1. Root and rhizome weights in relation to clipping frequency.

The weights of the rhizomes of *Digitaria tricholaenoides* suffered relatively slight reduction due to increased intensity of defoliation; the differences would, however, not include any possible decrease due to reduction of total rhizome length. Whilst fertilizer treatment seems to have increased the root weights of *Tristachya hispida*, *Eragrostis chalcantha* and *Digitaria tricholaenoides*, at least under conditions of moderate defoliation, the differences due to fertilizer treatment are mostly insignificant with the roots of *Trachypogon plumosus* and *Brachiaria serrata*, and the rhizomes of *Digitaria tricholaenoides*. The effect of fertilizer treatment was, thus, not very consistent in the various species studied, though fertilizer treatment considerably increased the total herbage yields (23). With excessive defoliation, application of fertilizer tended to reduce the root weights, which would agree with the findings of other workers previously mentioned (5, 6, 8). In an earlier investigation, where the root bulk from whole quadrats was determined, the writer (22) could detect no effects of fertilizers on root growth, and it was concluded "that measurable effects of fertilizers on root development should not necessarily be expected in every case where the same treatments significantly influence the herbage yield."

Since many grasses send some of their roots down to a considerable depth, and roots were collected only to a depth of four inches, it may be argued that the reported root weights are not reliable. In 1941, however, two unclipped quadrats, each one square metre in extent, were dug up in the experimental area, and the total weight of roots determined in four-inch layers to a depth of twenty inches. The results are shown in Table III.

TABLE III.

ROOT WEIGHTS IN DIFFERENT SOIL LAYERS.

Soil layer.	Grams air-dry Root Weight.	Percentage of total Root Weight collected (0-20").
0—4"	613	67·7
4—8"	107	11·8
8—12"	103	11·4
12—16"	59	6·5
16—20"	24	2·6
Total	906	100·0

The results indicate that the largest proportion (about 2/3) of the roots of these grasses occurs in the upper four inches of the soil, and that the root bulk rapidly decreases in lower soil levels. Hence, the root

TABLE IV.

SUGAR AND STARCH CONTENT OF ROOTS AND RHIZOMES.

EXPRESSED AS PERCENTAGES OF COMBUSTIBLE DRY MATTER.

Number of cuts per year.	Unfertilized.				Fertilized.			
	Re- ducing Sugars	Non-re- ducing Sugars	Starch	Total	Re- ducing Sugars	Non-re- ducing Sugars	Starch	Total
<i>Trachypogon plumosus</i> : Roots.								
1	0.67	6.05	1.59	8.31	0.67	7.25	1.52	9.44
2	0.53	5.07	1.05	6.65	0.85	6.35	1.59	8.79
4	0.48	3.16	0.94	4.58	0.62	3.82	2.89	7.33
9	0.48	0.41	0.83	1.72	0.57	3.23	0.61	4.41
16	0.65	0.56	0.87	2.08	0.00	0.93	0.47	1.40
<i>Tristachya hispida</i> : Roots.								
1	0.60	2.89	8.53	12.02	0.61	3.50	6.62	10.73
2	0.69	2.81	6.88	10.38	0.63	3.06	6.85	10.54
4	0.74	2.31	5.00	8.05	0.85	2.67	5.10	8.62
9	0.29	0.55	0.66	1.50	0.29	0.55	0.56	1.40
16	0.16	0.08	0.64	0.88	0.33	0.14	0.73	1.20
<i>Eragrostis calcantha</i> : Roots.								
1	0.48	3.51	1.38	5.37	0.43	4.66	1.16	6.25
2	0.48	3.34	0.41	4.23	0.51	3.45	0.51	4.47
4	0.27	3.05	0.39	3.71	0.37	2.61	0.28	3.26
9	1.00	2.50	0.56	4.06	0.47	3.97	0.18	4.62
<i>Brachiaria serrata</i> : Roots.								
1	0.67	5.07	1.91	7.65	0.71	4.31	2.81	7.83
2	0.49	5.41	0.88	6.78	0.52	3.53	0.20	4.25
4	0.53	2.14	0.60	3.27	0.08	1.79	0.46	2.33
9	0.19	2.66	0.32	3.17	0.00	2.11	0.87	2.98
16	0.32	0.29	0.54	1.15	0.87	0.66	0.56	2.09
<i>Digitaria tricholaenoides</i> : Roots.								
1	1.02	4.30	0.85	6.17	1.11	7.73	0.51	9.35
2	0.79	4.30	0.74	5.83	1.18	4.44	0.56	6.18
4	0.74	3.85	0.58	5.17	0.80	5.85	0.49	7.14
9	0.36	0.74	0.80	1.90	0.06	0.73	0.43	1.22
16	0.46	1.01	0.70	2.17	0.00	0.36	0.65	1.01
<i>Digitaria tricholaenoides</i> : Rhizomes.								
1	0.42	1.00	1.55	2.97	0.46	1.16	0.79	2.41
2	0.38	0.56	1.30	2.24	0.64	1.36	0.91	2.91
4	0.39	0.58	1.75	2.72	0.62	1.86	0.83	3.31
9	0.28	0.18	0.91	1.37	0.15	0.18	0.61	0.94
16	0.29	0.01	1.37	1.67	0.30	0.30	0.84	1.44

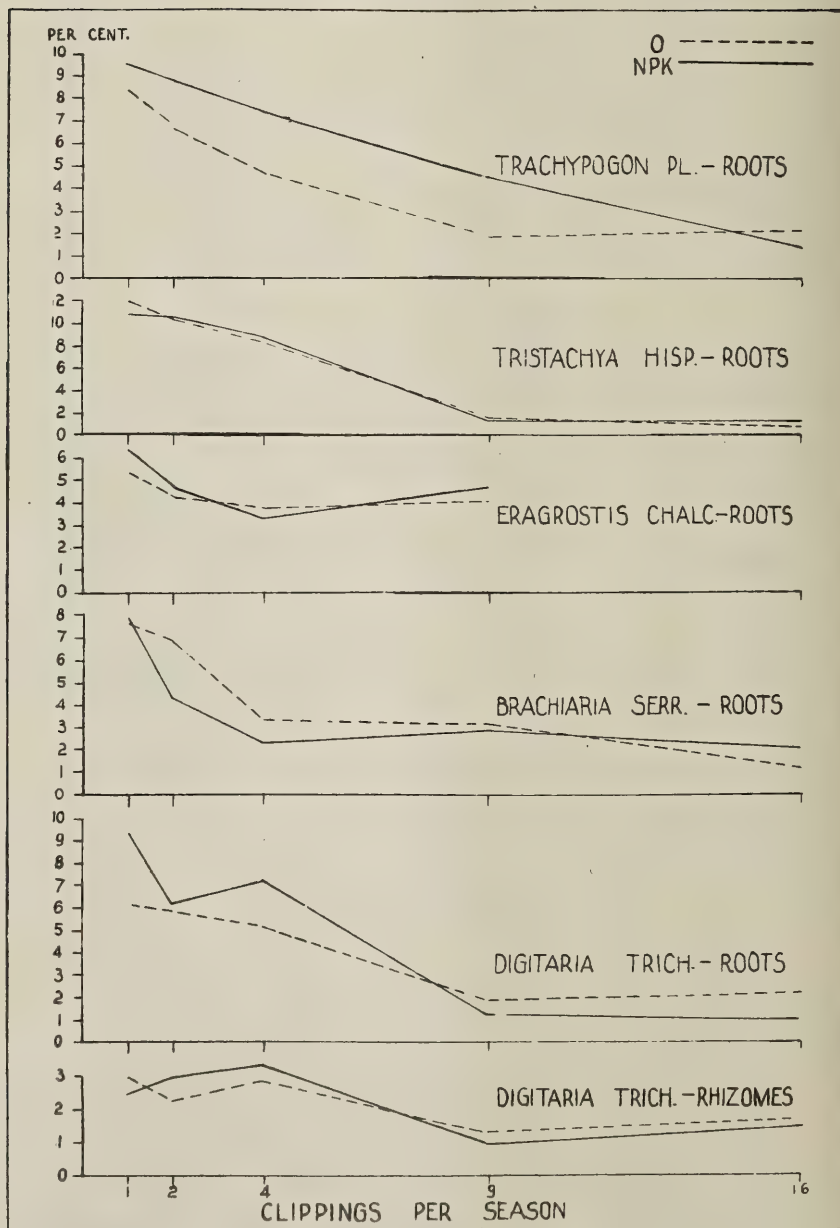


FIG. 2. Combined percentages of sugars and starch in roots and rhizomes, in relation to clipping frequency.

weights reported in this paper, though only being relative, can be regarded as representative and comparable.

Sugar and Starch Content.—Table IV gives the percentages of sugars and starch in the roots and rhizomes collected. It is evident that these compounds decreased in roots and rhizomes with the frequency of clipping. Though the different types of storage carbohydrates (reducing sugars, non-reducing sugars and starch) were not always affected by the various clipping treatments in the same way or to the same extent, the total percentages of sugars and starch (Fig. 2) definitely decreased with the number of clippings per season. In some cases the percentage of carbohydrates was somewhat higher in the roots of frequently cut plants than in the roots of plants cut fewer times. Thus, in *Eragrostis chalcantha* the combined percentages of sugars and starch in the roots of plants clipped nine times a season exceeded those in the roots of plants clipped four times a year; no analysis could be carried out on the roots of *Eragrostis* plants cut sixteen times a year on account of the small amounts of root material recovered in this treatment. The significance of the apparent increase in carbohydrates with increased clipping frequency in some of the species will be discussed below. Fertilizer exerted, on the whole, little influence on the percentages of sugars and starch in the roots, with the possible exception of *Trachypogon plumosus*, where it increased the carbohydrate content under most conditions of defoliation.

Some interesting differences are shown between the various species as regards the occurrence and relative proportions of these reserve carbohydrates, largely confirming earlier results of the author (21, 22). In the storage organs of all species investigated reducing sugars occurred in considerably smaller amounts than non-reducing sugars. Whilst *Tristachya hispida* was found to store more starch in its roots than non-reducing sugars, the roots of the other grasses contained non-reducing sugars in excess of starch. The respective ratios of these carbohydrates were, however, frequently altered or even reversed under the abnormal conditions of excessive defoliation. In the rhizomes of *Digitaria tricholaenoides* fertilizer treatment changed the proportion of non-reducing sugars to starch. Thus in the rhizomes of unfertilized plants starch exceeded non-reducing sugars under all conditions of defoliation, but in the fertilized plants the percentages of starch were lower than those of non-reducing sugars, at least with one, two and four clippings per season.

Acid-hydrolysable Polysaccharides.—In contrast to sugar and starch contents, the percentages of acid-hydrolysable polysaccharides in the roots and rhizomes (Table V) remained largely unaffected by frequency of clipping. The fluctuations were generally small and rather irregular,

TABLE V.
ACID-HYDROLYSABLE POLYSACCHARIDES IN ROOTS AND RHIZOMES.
EXPRESSED AS PERCENTAGES OF COMBUSTIBLE DRY MATTER.

Number of cuts per season.		1	2	4	9	16
Trachypogon pl., Roots	O	17.9	17.5	18.9	19.1	21.4
	NPK	17.5	17.7	17.5	18.9	18.5
Tristachya hisp., Roots	O	19.3	17.2	13.5	22.9	22.3
	NPK	17.9	16.3	17.5	22.6	20.8
Eragrostis chalc., Roots	O	21.8	20.3	19.3	22.1	—
	NPK	20.4	20.5	21.2	19.3	—
Brachiaria serr., Roots	O	19.9	22.9	21.6	20.3	21.7
	NPK	18.0	16.4	14.5	16.9	14.7
Digitaria trich., Roots	O	15.6	15.5	18.7	16.9	14.7
	NPK	18.2	16.8	17.0	18.2	21.3
Digitaria trich., Rhizomes	O	26.4	23.3	26.2	27.3	24.9
	NPK	27.4	27.9	26.1	26.6	27.6

and must be put down to certain inaccuracies of the method employed in determining these substances, which are often referred to as "hemicelluloses". Similarly, Aldous (1), McCarty (9) and Weinmann (22) found that clipping of the herbage did not reduce the percentages of acid-hydrolysable polysaccharides in the roots. It can, therefore, be concluded that these substances function in the roots mainly as structural materials, but cannot be utilised as food reserves. This view has also been expressed previously by McCarty (10) and by McCarty and Price (11). A noteworthy feature is that the more woody character of the rhizomes of *Digitaria tricholaenoides* is reflected by a higher content in acid-hydrolysable polysaccharides and a lower proportion of reserve carbohydrates as compared with the roots of the same and the other species of grasses.

Combined Amounts of Sugars and Starch.—Sugars and starch were reduced by frequent clipping not only in percentage but even more in actual amount since the root weights likewise decreased with the frequency of defoliation (Table VI and Fig. 3). In most cases where sugars and starch increased in percentage with increased frequency of clipping they still decreased considerably in actual amount, as shown, for instance, by *Eragrostis chalcantha* when four and nine clippings per season are compared. The apparent increase in the percentages of sugars

TABLE VI.

COMBINED AMOUNTS OF SUGARS AND STARCH IN ROOTS AND RHIZOMES.

MILLIGRAMS SUGARS AND STARCH IN ROOTS PER ONE SQUARE DECIMETRE BASAL AREA.

Number of cuts per season.		1	2	4	9	16
Trachypogon pl. ..	O	399	357	128	15	14
	NPK	635	493	220	28	6
Tristachya hisp. ..	O	590	675	310	38	20
	NPK	817	1,010	632	26	15
Eragrostis chal. ..	O	196	155	90	11	—
	NPK	462	443	80	12	—
Brachiaria serr. ..	O	780	1,040	55	20	25
	NPK	963	477	26	32	21

MILLIGRAMS SUGARS AND STARCH IN ROOTS AND RHIZOMES OF *Digitaria trich.* PER ONE METRE RHIZOME LENGTH.

Number of cuts per season.		1	2	4	9	16
Roots	O	37.6	34.4	24.8	5.1	3.9
	NPK	146.8	100.8	70.7	3.2	0.9
Rhizomes	O	320	240	293	108	136
	NPK	326	384	261	64	90

and starch in this species between four and nine clippings is easily explained : with nine clippings many of the depleted and weakened roots died and subsequently decomposed. This proportion of the roots was naturally lost, whilst the remaining less affected root portion possessed a higher percentage of sugars and starch than the bigger mass of roots left intact in the quadrats cut four times per season.

The lowest amounts of sugars and starch were present in all cases with the highest number of clippings employed, except in the rhizomes of *Digitaria tricholaenoides*, where somewhat higher amounts were found with sixteen cuts per year than with nine. No other explanation can be given for this than that it may be due to a sampling error or to the fact that in this species the values were based on rhizome length instead of

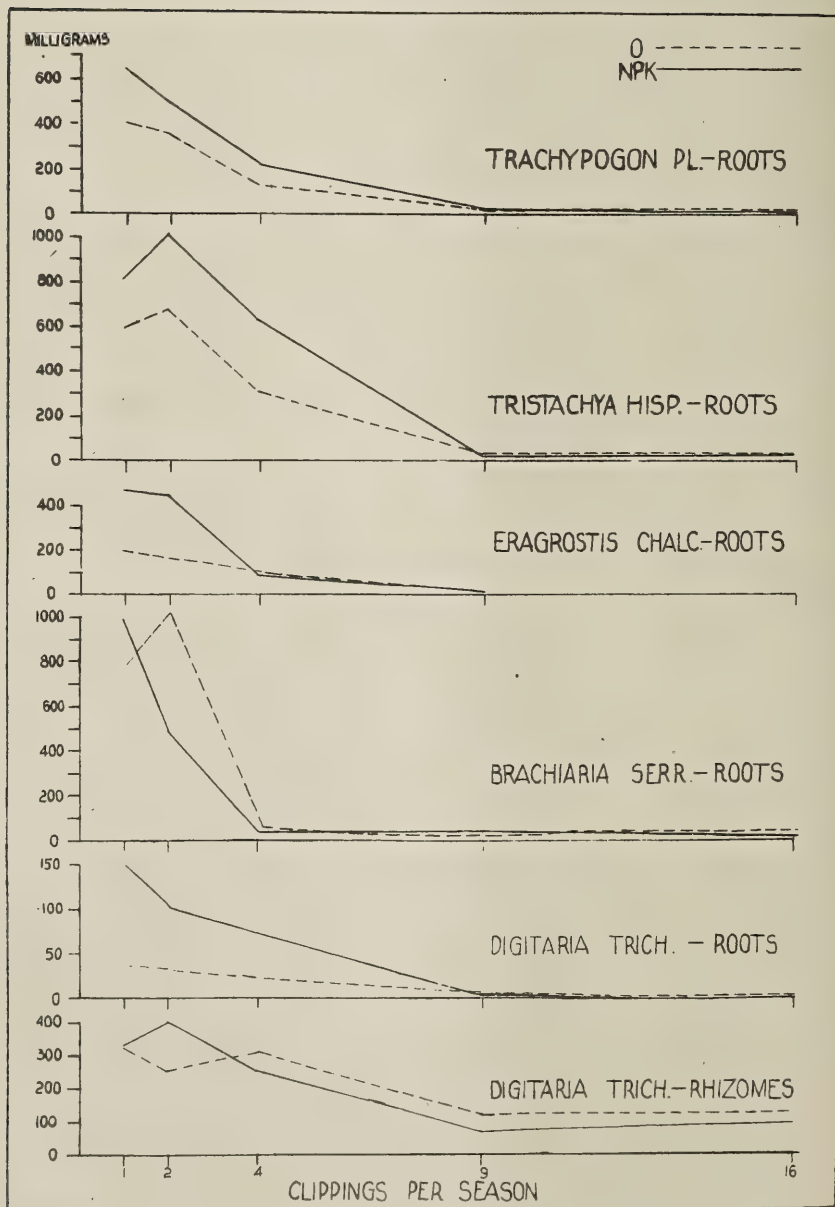


FIG. 3. Combined amounts of sugars and starch in roots and rhizomes, in relation to clipping frequency.

on basal area. The combined amounts of sugars and starch in the rhizomes of the *Digitaria* plants cut nine or sixteen times a year were, however, in either case still considerably lower than in the rhizomes of less frequently clipped plants. Even so it would appear that the rhizomes of *Digitaria tricholaenoides* responded to the clipping treatments in a different way to the roots of this and the other species.

Frequent clipping lowered the rhizome weights of *Digitaria tricholaenoides* and their carbohydrate content to a considerably lesser extent than it did in the case of the roots of all species. Clipping sixteen times per season reduced the combined amounts of sugars and starch in the roots of all species to a level approximating zero. The rhizomes of *Digitaria tricholaenoides*, however, retained a relatively large residue of reserve carbohydrates under the same severe conditions of defoliation. In spite of the low percentages of these substances it seems that *Digitaria tricholaenoides* possesses in its rhizomes considerable stores of reserve foods. This, together with its prostrate habit which protects the plant to a certain extent from unduly severe defoliation by grazing animals, may partly account for the fact that "the spreading of *Digitaria tricholaenoides* is encouraged by comparatively heavy grazing" (20). Graber (3) pointed out that plants with prostrate growth habit are more resistant to close mowing or grazing than erect plants, since a greater portion of the total leaf area is left intact after each defoliation. In the present experiment care was taken to remove all leaves uniformly at every cutting in all species tested. Hence, it may be concluded that the stores of carbohydrates in the rhizomes of *Digitaria tricholaenoides* are so large that they will not suffer the same degree of depletion by a cutting treatment which will almost completely exhaust the storage organs of the other species studied.

The combined amounts of sugars and starch were under conditions of moderate defoliation in most cases (except *Brachiaria serrata*) higher in the roots of fertilized plants than in those from unfertilized plots, but with excessive defoliation this was largely reversed. The fact that the residues of the combined amounts of sugars and starch in the roots of very frequently clipped plants were lower in the NPK-series than in the O-series seems to support the view that fertilizer treatment tends to aggravate the depletion of organic reserves brought about by frequent clipping (5, 6, 8). From the practical point of view, however, these differences appear to be mostly small and insignificant; also, no such effect could be observed in *Eragrostis chalcantha*, though here the amounts of roots remaining after sixteen clippings per season were too small to be determined accurately or to be analysed. At any rate, it may be safely

said that application of fertilizers was not able to counteract the depletion of root reserves caused by frequent clipping.

Exhaustion of Root Reserves in Relation to Herbage Growth.—The reduction in root weights and the exhaustion of organic reserves by excessive defoliation was associated with corresponding reductions of the total herbage yields, which were progressively diminished with increased frequency of clipping in both seasons. The yield reduction in the quadrats cut nine or sixteen times a season was more pronounced in the second than in the first year of treatment, indicating a cumulative and permanent effect. On the fortnightly clipped quadrats growth and regeneration stopped almost completely in the later half of the second season; many of the plants had apparently been killed by the severe treatment of defoliation (23). In fact, on these quadrats a number of plants had disappeared altogether by the time their roots were to be harvested, and few or no roots were found, since the plants had died and decomposed. This was particularly the case with *Eragrostis calcantha*, and is probably due to the fact that this species possesses a rather small and superficial root system. In this species 80 per cent. of the marked plants had disappeared completely in the quadrats subjected to cutting at fortnightly intervals, and even in the quadrats clipped at monthly intervals the loss was 40 per cent.

As previously pointed out by the writer (22), the reduction of root weights and the depletion of carbohydrate reserves in the roots by excessive defoliation is mainly due to two causes. Frequent clipping at short intervals will not permit of the normal storage of root reserves, since such storage usually takes place during the later part of the growing period, i.e. after flowering and during maturation (21). Secondly, the frequent repetition of the shooting process brought about by excessive clipping will result in an increased mobilisation and upward translocation of existing root reserves. In this way, excessive defoliation will gradually lead to carbohydrate starvation, reduced vigour and power of regeneration, and in extreme cases to the death of the plants.

SUMMARY.

The results are reported of an experiment designed to test the effects of clipping frequency, with and without fertilizer treatment, on root development and carbohydrate reserves of five important South African Highveld grasses growing under natural conditions. The species tested were *Trachypogon plumosus*, *Tristachya hispida*, *Eragrostis calcantha*, *Brachiaria serrata* and *Digitaria tricholaenoides*. Five different clipping

treatments were employed, namely cutting once, twice, four, nine and sixteen times per season for two years.

Increased frequency of clipping significantly reduced the root and rhizome weights and lowered the percentages of reducing sugars, non-reducing sugars and starch in these organs. The percentage of acid-hydrolysable polysaccharides remained unaffected by the frequency of clipping.

Fertilizer treatment increased the root weights of some of the species under conditions of moderate defoliation, but had generally little effect on the carbohydrate content.

Cutting at fortnightly intervals (or sixteen times per season) for two years led to an almost complete exhaustion of root reserves and to the death of many plants. Fertilizer treatment was not only unable to counteract these effects of excessive defoliation, but rather tended to aggravate them.

Weights and carbohydrate content of the rhizomes of *Digitaria tricholaenoides* were found to be less affected by frequent clipping than those of the roots of the same and other species.

The depletion in root reserves brought about by frequent clipping was associated with corresponding reductions in the herbage yields.

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